

ARTHROPODS IN URBAN HABITAT FRAGMENTS IN SOUTHERN CALIFORNIA: AREA, AGE, AND EDGE EFFECTS

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Abstract. The distribution of non-ant arthropods was examined in 40 urban habitat fragments in coastal San Diego County, California, USA, to look for effects of fragmentation, proximity to developed edge, and the non-native Argentine ant (*Linepithema humile*). Arthropods were sampled with pitfall traps and by vacuum sampling from California buckwheat shrubs (*Eriogonum fasciculatum*). Individual arthropods were identified to order and Recognizable Taxonomic Unit (RTU), or morphospecies. At the fragment scale we looked for correlations in the point diversity and abundance of arthropods as a function of the age and area of the fragment being sampled. At the scale of the individual sample points we looked for correlations of abundance and diversity with variables that describe the species composition of the shrub vegetation and disturbance. As indicators of disturbance we used the cover of native woody and exotic non-woody vegetation, the distance to the nearest developed edge, and the abundance of Argentine ants. The following patterns were found: (1) In general, arthropods showed a fragmentation effect with point diversity and abundance positively correlated with fragment area and negatively correlated with fragment age. (2) The pitfall samples were dominated by three primarily non-native orders, Isopoda (pillbugs), Dermaptera (earwigs), and Blattaria (roaches). Over 35% of all pitfall-captured arthropods belonged to four species in these orders. Dermaptera and Blattaria increased in abundance in smaller and older fragments, respectively. Isopod abundance, in contrast, was unrelated to fragment attributes. None of these groups appeared to be associated with edges, but were distributed throughout the fragments. (3) Point diversity and abundance in ground-active spiders appears to be enhanced by fragmentation. (4) Total pitfall RTU richness and abundance, and abundance or richness in the Coleoptera (vacuum), Diptera, non-ant Hymenoptera, Hemiptera, Microcoryphia, and Acarina had significant partial negative correlations with Argentine ant abundance. The Diptera and Coleoptera had this negative partial relationship with the Argentine ants despite the fact that both they and the ants were positively associated with edges. (5) In general, diversity in most orders was higher in sampling locations dominated by coastal sage scrub habitat than in those with appreciable cover of chaparral shrub species. (6) There was a strong seasonal variation in abundance and diversity in most orders. Diversity and abundance were highest in spring, intermediate in winter, and lowest in the fall. (7) Although higher trophic levels are often considered to be more sensitive to fragmentation, two groups of arthropod predators, spiders and carabid beetles, increased in abundance in older fragments. Abundance of these predators was positively correlated with the abundance of Argentine ants and the non-native Isopods, Dermaptera, and Blattaria.

Key words: Argentine ant; arthropods; edge effects; exotic species; habitat fragmentation; insects; invasion; *Linepithema humile*.

INTRODUCTION

The ecological effects of habitat fragmentation are complex, diverse, and pervasive because fragmentation affects animal and plant populations via a number of interacting pathways (Wilcove et al. 1986, Robinson et al. 1992, Didham et al. 1998a). Area effects manifest through the initial sampling effect (Bolger et al. 1991) and through the effect of area on population sizes and

rates of stochastic extinction. Isolation effects occur when the intervening human-modified matrix is relatively impermeable to dispersal. This may result in relaxation, or faunal collapse in the extreme of zero recolonization (Brown 1971, Soulé et al. 1979). Edge effects are spillover effects from the surrounding human-modified matrix that cause physical gradients in light, moisture and wind velocity, increased exposure to invasive human commensal species, and increased density of “edge species” (Murcia 1995). The direct effects of area reduction, isolation, and edge can lead

to secondary effects (also called cascading or trophic effects), whereby the direct effects of fragmentation on predators, parasites, competitors, resource species, or mutualists in turn affect other species with which these interact. Our understanding of fragmentation has been hampered by the inability to isolate the effects of these different phenomena on the biota.

The effect of habitat fragmentation on arthropods is relevant to the conservation of biological diversity from several perspectives. Over 90% of all species may be arthropods (Erwin 1982); they comprise the most diverse taxa in most ecosystems and may play important functional roles in ecosystem processes. Fragmentation, or other habitat disturbance, has been shown to affect arthropods, their trophic interactions and their ecosystem functions. These interactions and functions include pollination (Powell and Powell 1987, Jennersten 1988, Becker et al. 1991, Aizen and Feinziger 1994a, b), predator-prey interactions (Kareiva 1987, Burke and Nol 1998), parasitoid-host interactions and biological control (Kruess and Tscharnake 1994), decomposition (Klein 1989), and plant-herbivore interactions (Burkey 1993).

Arthropod response to fragmentation could have important consequences for vertebrate insectivores, some of which are the focus of conservation efforts. With few exceptions, mechanistic studies of the effect of habitat fragmentation on birds and other vertebrates have concentrated on top-down effects of predation and nest parasitism (Wilcove 1985, Robinson et al. 1995). However, the bottom-up effect of arthropod prey availability may also be important (Burke and Nol 1998).

While generalities about vertebrate responses to habitat fragmentation have been made, similar generalizations are just emerging for arthropods (Didham 1998a). One generalization is that invertebrate diversity increases near forest edges (Didham 1997). Several studies in patches of forest (Didham 1997, Helle and Muona 1985) and heathland (Webb et al. 1984, Webb 1989) have shown increased diversity near edges in some arthropod orders. In some cases this is due to an increase in generalist, edge species (Webb et al. 1984, Webb 1989, Didham 1997), or the spillover of species that specialize on adjacent habitat types (Duelli et al. 1990, Shure and Phillips 1991).

In this study, we examined patterns of diversity and abundance of arthropods in a set of urban scrub habitat fragments in San Diego, California, USA that have been the site of previous studies of the effect of fragmentation on birds (Soulé et al. 1988, Bolger et al. 1991, Langen et al. 1991, Crooks et al., *in press*), rodents (Bolger et al. 1997a), plants (Alberts et al. 1993), and ants (Suarez et al. 1998). For scrub habitat specialists in these taxa, species richness increases with fragment area and declines with fragment age. The latter relationship implies that local extinctions exceed recolonizations across the urban matrix. The existence of this extinction-recolonization imbalance is sup-

ported for bird, rodent, and ground foraging ant species by the observation that they are less diverse in these fragments than in similar-sized plots in continuous blocks of habitat (Bolger et al. 1991, Bolger et al. 1997a, Suarez et al. 1998). More direct evidence of this relationship in birds is that between 1986 and 1996 the number of documented local extinctions was twice the number of recolonizations (Crooks et al., *in press*).

Island biogeographic treatments of habitat fragmentation focus on the relationship between stochastic extinction and recolonization (MacArthur and Wilson 1967, Brown 1971). However, when fragmentation results from the intervention of intense human land uses such as urbanization, edge effects and other anthropogenic disturbance are likely to be significant influences on abundance and extinction rates. Reduced diversity observed in older fragments, the "age effect", may be a result of both types of effects.

The effect of disturbance in these fragments is most apparent in the percent cover (Soulé et al. 1988) and species diversity of native shrub vegetation which decline with fragment age while non-native plant diversity increases (Alberts et al. 1993). These changes are probably due to increased mechanical disturbance, however modified fire frequency and other undocumented physical and ecological changes could also contribute. The biota of these fragments are also exposed to human commensal species (Alberts et al. 1993, Suarez et al. 1998, Crooks and Soule 1999) and increases in "edge" species (Bolger et al. 1997b). These disturbance factors should play a role in determining the diversity and abundance of arthropods in these fragments.

A potentially potent edge effect in urban habitat fragments in coastal southern California is exposure to the exotic Argentine ant (*Linepithema humile*). Argentine ants have become established in Mediterranean climates worldwide (Majer 1994, Passera 1994) and have been implicated in the decline of native ants in a number of locations (Erickson 1971, Ward 1987, Majer 1994, Holway 1995, Cammell et al. 1996, Human and Gordon 1996). Suarez et al. (1998) have documented that Argentine ants invade habitat fragments in San Diego and appear to contribute to the decline of most native ants. Argentine ants enjoy interference and exploitative competitive advantages over native ants (Human and Gordon 1996, Holway 1999) and have higher worker densities possibly due to reduced intraspecific competition in this species (Holway et al. 1998). Several studies have implicated Argentine ants, or other exotic ants, in the decline of non-ant arthropods (Porter and Savigno 1990, Cole et al. 1992, Human and Gordon 1997), while others have found no effect (Holway 1998b).

Most studies of the effect of fragmentation on arthropods have focused on single species or small groups of species. Focused studies are clearly valuable, but these species may be unrepresentative (see review

in Didham 1997). In this study, we used pitfall and vacuum sampling to examine a broad sample of the arthropod community. This has the potential advantage of revealing general patterns of diversity and exposing interactions among arthropod groups or between native and non-native species. However, due to the great diversity of species, genera, families, and orders involved, it requires a coarse taxonomic approach.

Specifically, we evaluated the following hypotheses: (1) point diversity and abundance of arthropods decreases with decreasing fragment area, and (2) decreases with increasing fragment age; (3) predator species are particularly sensitive to fragment area and age (Terborgh and Winter 1980); (4) common non-native species increase in abundance with decreasing fragment area and increasing fragment age; (5) Argentine ants reduce the diversity and abundance of non-ant arthropods (Cole et al. 1992, Human and Gordon 1997); and (6) arthropod diversity and abundance increases near edges (Didham 1997).

METHODS

Pitfall sampling

Samples were collected in arrays of five pitfall jars (250-mL jars, 60 mm inside diameter) placed at ~100 m intervals along a transect parallel to the longest axis of the habitat fragment (see Suarez et al. 1998). Pitfalls were located in stands of native shrub vegetation and arrays were distributed so that they varied in distance from the fragment edge. The number of arrays varied with the size of the fragment and ranged from 1 to 11 per fragment. The five jars in an array were placed in a pattern resembling the five on a die with the corner jars being 20 m apart. Each jar was half-filled with a 50:50 mixture of water and nontoxic antifreeze. The antifreeze prevented evaporation and acted as a preservative. The jars were buried with the rim of the jar flush with the ground surface. Jars were opened for 5-d sampling periods during each of three seasons: fall (August–November 1995), winter (December 1995–February 1996) and spring (April–July 1996). The order in which fragments were sampled was randomized within each season. The contents of the five jars in each array were pooled to form the sample for that point. Arthropods were separated from debris, washed, and stored in 70% ethanol. Data on the ants in these samples are reported in Suarez et al. (1998).

Vacuum sampling

We sampled arthropods on California buckwheat (*Eriogonum fasciculatum*) shrubs at the same points as the pitfall arrays. Along with *Artemisia californica*, buckwheat is the codominant shrub species in coastal sage scrub. The crown and base of the shrubs were vacuum-sampled with a modified leaf-blower (designed by R. Redak; Buffington and Redak 1998) for 1 min. The nozzle of the vacuum was moved through

the foliage at a constant rate and several individual shrubs were vacuumed in each 1-min sample. Samples were collected during daylight hours in the period 6 May to 27 May 1996. Samples were transferred to storage bags, placed on ice, and sent to the lab at Dartmouth College for processing. In the lab arthropods were manually separated from debris and stored in 70% ethanol.

Arthropod classification

Individual arthropods were identified to order. Then, within each sample, all individuals were categorized into Recognizable Taxonomic Units (RTU's, Oliver and Beattie 1993), or morphospecies. Given the high level of diversity and the large number of samples collected (>45 000 individual arthropods classified), classification to the species level was not possible. The number of RTU's has been used as a surrogate for species richness by a number of investigators (Oliver and Beattie 1993, Weaver 1995, Ingham and Samways 1996, Didham et al. 1998a). Ninety percent agreement has been found between RTU classification by nonspecialist technicians and specialist taxonomists (Oliver and Beattie 1993). All RTU assignments were made by a single individual with a Master of Science degree in Entomology. Common names of the orders mentioned in the text are given in Table 1.

Fragment variables

The same forty fragments used in Suarez et al. (1998) were used in this study (Fig. 1, Table 2). Many of these were also used in previous studies (Soulé et al. 1988, Bolger et al. 1991, 1997a, Alberts et al. 1993). Most are remnants of dendritic drainages that have been isolated by development sometime in the last 90 years. The predominant habitat type in these fragments is coastal sage scrub with smaller amounts of coastal chaparral. Fragment age (AGE) (years since insularization) was determined from dated aerial photographs and building permit records (Soulé et al. 1988, Suarez et al. 1998). Most of the fragments are long and narrow, potentially increasing the importance of edge effects (Fig. 1). We use the area of shrub vegetation in the fragment as our measure of fragment area (AREA) because it is a better measure of habitat area and a better predictor of coastal sage scrub arthropod, bird, and rodent diversity than is total fragment area (Soulé et al. 1988, Bolger et al. 1997a). Fragments range in composition from 10–90% cover of coastal sage scrub and chaparral (Suarez et al. 1998). The remaining area was typically disturbed and dominated by exotic grasses and herbs. AREA was derived by multiplying the percent cover of native shrub vegetation by total fragment area. Older fragments tend to be smaller than younger fragments by this measure of fragment area because of the lower percent shrub cover in older fragments (Soulé et al. 1988). Thus, part of the effect of fragment age is a loss of habitat through time; by using a measure of shrub habitat area rather than total fragment area we

TABLE 1. Mean number of individuals (percentage) and RTU's (percentage) in arthropod orders per spring vacuum and pitfall sample.

Order	Common name	Vacuum samples		Pitfall samples	
		Abundance	RTU richness	Abundance	RTU richness
Araneae	Spiders	10.50 (16.22)	4.63 (19.46)	16.86 (10.59)	8.03 (22.37)
Scorpiones	Scorpions			0.08 (0.05)	0.08 (0.22)
Pseudoscorpiones	Pseudoscorpions			0.07 (0.05)	0.06 (0.16)
Solfugae	Windscorpions			0.46 (0.29)	0.25 (0.70)
Opiliones	Harvestmen			0.03 (0.02)	0.03 (0.07)
Acarina	Mites	0.03 (0.04)	0.03 (0.12)	27.80 (17.47)	2.03 (5.64)
Isopoda	Sowbugs	0.02 (0.04)	0.01 (0.05)	48.15 (30.26)	1.53 (4.25)
Diplopoda	Millipedes			0.05 (0.03)	0.05 (0.15)
Chilopoda	Centipedes			0.13 (0.08)	0.12 (0.33)
Collembola	Springtails			4.41 (2.77)	0.78 (2.16)
Microcoryphia	Jumping Bristletails	0.06 (0.09)	0.05 (0.19)	7.09 (4.45)	0.83 (2.31)
Thysanura	Silverfish			0.07 (0.04)	0.05 (0.15)
Orthoptera	Grasshoppers	0.32 (0.50)	0.23 (0.97)	1.62 (1.02)	1.01 (2.80)
Mantodea	Mantids	0.01 (0.02)	0.01 (0.05)	0.02 (0.01)	0.02 (0.05)
Blattaria	Cockroaches	0.01 (0.02)	0.01 (0.05)	9.81 (6.16)	0.93 (2.58)
Isoptera	Termites			0.06 (0.04)	0.02 (0.05)
Dermaptera	Earwigs	0.04 (0.06)	0.03 (0.12)	1.05 (0.66)	0.30 (0.82)
Embiidina	Web-spinners			0.20 (0.12)	0.16 (0.44)
Psocoptera	Psocids	1.10 (1.71)	0.71 (2.99)	1.11 (0.69)	0.62 (1.72)
Hemiptera	Bugs	15.13 (23.36)	2.09 (8.79)	2.11 (1.33)	1.20 (3.35)
Homoptera	Hoppers	14.83 (22.91)	5.50 (23.12)	4.30 (2.70)	3.11 (8.67)
Thysanoptera	Thrips	0.02 (0.04)	0.02 (0.07)	0.40 (0.25)	0.24 (0.68)
Neuroptera	Lacewings	0.06 (0.10)	0.06 (0.27)	0.04 (0.02)	0.04 (0.11)
Coleoptera	Beetles	12.85 (19.85)	4.42 (18.56)	15.82 (9.94)	4.99 (13.89)
Siphonaptera	Fleas			0.11 (0.07)	0.09 (0.24)
Diptera	Flies	2.72 (4.20)	1.88 (7.92)	9.49 (5.96)	3.82 (10.65)
Lepidoptera	Moths and Butterflies	2.60 (4.01)	1.41 (5.93)	0.64 (0.41)	0.53 (1.47)
Hymenoptera (non-ant)	Wasps and Bees	4.43 (6.84)	2.70 (11.35)	7.18 (4.51)	5.01 (13.95)
Totals		64.75	23.80	159.14	35.90

are choosing to ignore this component of the age effect. Total fragment area was measured from digitized scaled aerial photographs taken in 1995. The percent cover of native shrub vegetation was estimated by inspection of aerial photographs and vegetation surveys within each fragment (Suarez et al. 1998).

Sample point variables

At each pitfall array location, the following measures of local habitat variation were measured on an area of 20 m radius (Table 3). A Braun-Blanquet (Kent and Coker 1992) categorical scale was used to classify sites as to the per cent cover of native shrubs (SHRUB), exotic non-woody vegetation (EXOTIC), and the cover of each shrub species. Our cover scale was 0 (<1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), 5 (76–100%). Twelve common shrub species were scored for abundance: California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), black sage (*Salvia mellifera*), California encelia (*Encelia californica*), lemonadeberry (*Rhus integrifolia*), laurel sumac (*Malosma laurina*), chaparral broom (*Baccharis pilularis*), manzanita (*Arctostaphylos glandulosa*), scrub oak (*Quercus dumosa*), chamise (*Adenostoma fasciculatum*), *Ceanothus* sp., and jojoba (*Simmondsia chinensis*).

A principal components analysis was performed on the shrub species cover data. The scores from the first

two axes (PC1 and PC2) were used in the multiple regression analyses described below. The Shannon-Wiener diversity index was also calculated from the shrub species data (SWDIV). Other variables measured included the distance from each sampling point to the nearest fragment edge (EDGEDIST) and the abundance of Argentine ants (AA) at each sampling point (ant data from Suarez et al. 1998).

Analysis

Data were analyzed at two spatial scales: among fragments and among sample points. As in previous studies of arthropod diversity, we tested for a fragmentation effect by comparing the mean diversity and abundance from multiple point samples within each fragment (mean point diversity and abundance) among fragments (Didham 1997, Didham et al. 1998a). Mean total arthropod abundance and RTU richness was compared among fragments as was the mean point abundance and RTU richness in each order. We compared among individual sample points to test for effects of the structure and composition of vegetation, edge proximity, and Argentine ants on diversity and abundance.

The distribution of abundance and RTU richness was log-normal for the more diverse orders (Coleoptera, Diptera, Araneae, Lepidoptera, Hemiptera, Homoptera, and non-ant Hymenoptera). For some or-



FIG. 1. Map of habitat fragments studied in coastal San Diego County, California, USA. Numbers refer to fragment numbers in Table 2. The two fragments not shown on the map, Oak Crest and Montanosa, are located in Encinitas, approximately 10 km north of the map area. White lines indicate highways, grey background indicates urbanized areas, and areas with predominantly native vegetation are in black.

ders RTU richness was low and could not be normalized, but abundance was log-normal. In these cases (Acarina, Microcoryphia, Dermaptera, Isopoda, Blattaria), only abundance was analyzed. The distribution of abundance in Dermaptera, Collembola, and Blattaria rendered them difficult to analyze at the among sample point scale. These orders were absent from a significant number of samples, and in the other samples their abundance was highly variable. Consequently, the abundance of these species was analyzed with bivariate Spearman rank correlations. Sixteen other arthropod orders were too uncommon to be

analyzed separately. These were still included in the total RTU, total orders, and total individuals counts. Analysis of the abundance and diversity of the ants in these samples is presented elsewhere (Suarez et al. 1998) so ants were not included here in total RTU richness and total abundance figures.

Among fragments: AREA and AGE multiple regression

To test for a fragmentation effect, we performed multiple regressions with mean total abundance, total RTU richness and order richness, and the RTU richness and

TABLE 2. List of habitat fragments surveyed including the area of shrub habitat within them, their age (years elapsed since isolation by development), and the number of points within each fragment that were sampled each season (see *Methods*).

Habitat number	Name	Area (ha)	Age (yr)	Number of points sampled			
				Fall	Winter	Spring (pitfall)	Spring (vacuum)
1	Florida	71.1	59	7	0	9	9
2	Chula Vista	90.7	3	4	6	5	5
3	Rice	66.5	3	3	9	9	0
4	Sandmark	32.5	29	10	0	8	9
5	34th Street	47.9	43	8	8	8	6
6	Balboa Terrace	36.6	43	9	0	5	6
7	Bonita Long	33.0	8	3	0	4	5
8	Terra Nova	40.0	10	4	7	6	6
9	Alta La Jolla	17.1	23	2	5	5	5
10	Home Depot	27.0	4	1	0	8	8
11	Kate Sessions	26.3	25	5	4	5	5
12	Zena	4.4	45	4	4	4	4
13	Sage View	8.9	19	2	3	3	3
14	Canon	2.3	67	5	3	5	3
15	Laurel	0.5	88	5	5	4	3
16	Pottery	4.8	23	2	3	5	4
17	32nd Street	1.4	65	4	3	4	4
18	Washington	2.3	83	7	2	5	5
19	Syracuse	6.1	27	3	2	2	4
20	47th Street	3.3	41	4	4	4	2
21	Paseo Del Rey	6.0	20	2	3	3	3
22	Baja	4.0	40	3	3	3	3
23	Raffee	4.0	28	2	0	1	2
24	Acuna	2.1	31	2	2	3	4
25	Juan	3.4	32	4	0	4	4
26	Edison	5.4	17	3	0	0	3
27	Telegraph	2.9	19	3	3	4	0
28	Chollas	1.6	45	2	2	2	1
29	Oak Crest	5.0	15	2	0	2	2
30	Chateau	3.1	29	3	2	3	2
31	Sundown	3.1	8	1	3	3	2
32	Spruce	0.4	95	3	3	3	1
33	60th Street	1.4	46	2	2	2	2
34	54th Street	2.0	29	2	2	2	3
35	Titus	0.3	86	5	5	1	1
36	Montanosa	2.2	11	2	0	2	2
37	El Mac	1.4	41	2	2	2	2
38	Poinsettia	0.6	59	2	2	1	2
39	Camino Coralino	0.3	29	2	0	2	3
40	Tarplant	0.3	3	1	1	1	1

abundance within individual arthropod orders as dependent variables and fragment AREA and AGE as the independent variables. If arthropod diversity and abundance decline as a consequence of fragmentation we would expect significant relationships between these diversity and abundance measures and fragment area (positive) and age (negative).

Among sample points: ANOVA

An area effect could be due to the increasing effect of edge in smaller fragments. To test for this, we grouped individual sample points into three categories: small fragments (29 fragments with <9 ha of shrub vegetation, 80 sample points, \bar{X} = 33.6 m from the edge, range 10–100 m), edge in larger fragments (within 100 m of fragment edge in 11 fragments with >17 ha of shrub vegetation, 37 sample points, \bar{X} = 51.4 m, range 20–80 m), interior of large fragments (32 sample points >100 m from the edge in the larger fragments,

\bar{X} = 180 m, range 100–500 m). All sample points in the small fragments were within 100 m of an edge due to small size of the fragments. Abundance and diversity among these three location types were compared with ANOVA. A significant post-hoc difference between edge and interior sites of large fragments was taken as evidence of an edge effect.

Among sample points: multiple regression

Factors other than fragment age, fragment area, and distance to an edge can affect arthropod diversity and abundance. Also, a variety of factors could vary continuously with edge distance. If these factors have opposing effects on arthropod abundance and diversity these effects could be obscured in the ANOVA results. To explore the proximate factors that influence arthropod diversity and abundance at the among sample point scale, we performed multiple linear regressions of total abundance, RTU and order richness, and the RTU rich-

TABLE 3. Names and definitions of independent variables used in statistical analyses.

Variable name	Variable description
AREA	Logarithm of the area of shrub habitat within the fragment
AGE	Logarithm of the number of years elapsed since the fragment was isolated by development
Among-sample point variables	
EXOTIC	Categorical percent cover of exotic grasses and herbs within 20 m radius of sample location
SHRUB	Categorical percent cover of native shrubs within a 20 m radius of sampling location
EDGEDIST	Log of the distance from the sampling location to the nearest developed edge
PC1	Scores from the first principal component on shrub species composition at each sampling location
PC2	Scores from the second principal component on shrub species composition at each sampling location
AA	The logarithm of the total number of Argentine ants captured at the sampling location
SWDIV	Shannon-Wiener diversity index calculated on the categorical cover values for shrub species

ness and abundance within individual arthropod orders on descriptors of vegetation and disturbance at each sampling site. The independent variables included a set that described the structure and composition of the woody vegetation (PC1, PC2, SWDIV, SHRUB) and a set that captured some elements of disturbance and edge effect (EXOTIC, EDGEDIST, AA). We used only the samples from the season of maximum diversity and abundance for each taxa in these analyses because in other seasons some orders were not abundant enough for analysis and because we felt these seasons were most representative of diversity in those taxa. This was spring for all but the Collembola and Dermaptera, which peaked in abundance in winter.

We used only the sample points from the 11 fragments >30 ha in total area. Smaller fragments are more likely to be dominated by among fragment scale variables such as AREA and AGE. Smaller fragments have no "interior" with regard to edge effects such as Argentine ant abundance (Suarez et al. 1998). For instance, all sample points in smaller fragments have moderate to high abundance of Argentine ants, while many points in the larger fragments have low to no Argentine ants. Restricting ourselves to the larger fragments restricts the range of the between fragment variables such as AREA and AGE yet maintains the range of the within fragment disturbance variables EDGEDIST, AA, and EXOTIC thus allowing us to isolate those effects. To aid in the interpretation of the multiple regressions the correlations among the independent variables are presented in Table 4.

TABLE 4. Simple Pearson correlations among sample point variables.

Variable	PC1	PC2	SWDIV	SHRUB	EXOTIC	EDGEDIST	AA
PC1	1.000						
PC2	-0.631*	1.000					
SWDIV	-0.007	0.065	1.000				
SHRUB	-0.190	0.255	0.269	1.000			
EXOTIC	0.044	-0.297	-0.018	-0.292	1.000		
EDGEDIST	0.133	0.178	-0.057	0.235	-0.444*	1.000	
AA	0.120	-0.410*	0.166	0.004	0.287	-0.511*	1.000

Notes: There were $n = 73$ sampling points used in the multiple regression analyses. See Table 3 for definitions of the variables.

* Significant at $\alpha = 0.05$ after sequential Bonferroni correction for 21 tests.

Sequential Bonferroni corrections were applied to all the correlation coefficients in each correlation table (Rice 1989). They were also applied when more than one regression or ANOVA analysis was performed on the same hypothesis. For the test of fragmentation effects on the total arthropod community, six tests were performed in each of the among fragment and among sample point analyses: total RTU richness, order richness, and total individuals in the spring pitfall and vacuum samples. For tests of fragmentation effects on individual orders, four tests were performed for each order in both the among fragment and among sample point analyses: abundance and RTU richness in the spring pitfall and vacuum samples were analyzed. Some orders were only tested in either the vacuum or the pitfalls, in these cases the correction factor was two. All statistical analyses were performed using JMP statistical software (SAS Institute, Cary, North Carolina, USA).

Predator analysis

To examine correlations in abundance between two ground-dwelling predator groups (spiders and carabid beetles) and non-native potential prey groups, we performed stepwise multiple regression analyses at the fragment and sample point levels. The independent variables in the among fragment analyses were AREA, AGE, and the abundance of Argentine ants, Isopoda, Dermaptera, and Blattaria. At the sample point scale, in addition to the non-native arthropod abundances, the variables PC1, PC2, SWDIV, EXOTIC, SHRUB, and

TABLE 5. Results of principal components analysis on the percent cover of major shrub species at each sample point.

Species	Loadings	
	PC1	PC2
<i>Adenostoma fasciculatum</i>	0.415	0.361
<i>Arctostaphylos glandulosa</i>	0.371	0.432
<i>Ceanothus</i> sp.	0.280	0.117
<i>Malosma laurina</i>	0.260	-0.141
<i>Salvia mellifera</i>	0.232	0.238
<i>Quercus dumosa</i>	0.221	-0.225
<i>Heteromeles arbutifolia</i>	0.120	-0.345
<i>Eriogonum fasciculatum</i>	0.110	-0.058
<i>Baccharis pilularis</i>	-0.183	-0.300
<i>Rhus integrifolia</i>	-0.244	0.022
<i>Encelia californica</i>	-0.278	0.331
<i>Simmondsia chinensis</i>	-0.301	0.382
<i>Artemisia californica</i>	-0.393	0.271
Cumulative percentage of variance	22.5	34.3

Note: The cumulative percentage of total variation carried by the first two components is presented as are the component loadings for each shrub species.

EDGEDIST were included in the analysis. We also analyzed the abundance of the most abundant carabid (CO-11, 1.5 cm) and the most abundant spider (AR-71, 3 mm) in the spring pitfall samples as a function of the abundance of Argentine ants using one-way ANOVA. The treatment was Argentine ant abundance with the following four levels: 0, 0-5, 5-15 and >15 ants per pitfall array.

To compare the species composition of the carabids and spiders between different sample point types (small, edge, interior) a subset of common or otherwise distinct carabid beetles (11 species) and spiders (12 species) were identified across samples. These species were assigned a unique identifying number and the presence and abundance of each in each sample was recorded. We calculated Jaccard binary similarity coefficients (Krebs 1989) between all pairs of sample points. The Jaccard coefficient is the number of species shared between the two samples divided by the total number of unique species present in the two samples. So, it can be thought of as roughly the proportion of species shared. Pairs of sample points were grouped according to the pairwise combination of site types (e.g., small fragment-large fragment similarity). The mean Jaccard coefficient was compared among the comparison types with Kruskal-Wallis nonparametric ANOVA; pairwise post-hoc comparisons were made using Bonferroni corrected Mann-Whitney *U* tests.

RESULTS

Principal components analysis

The first principal component separates sampling points that are typical coastal sage scrub from those with elements of Coastal Chaparral (Table 5). PC1 loads heavily positively on chaparral shrub species (*Adenostoma fasciculatum*, *Arctostaphylos*, and *Ceanothus*

sp.) and negatively on the coastal sage scrub species (*Artemisia californica*, *Encelia californica*, and *Rhus integrifolia*). PC2 separates sites that contained a mix of the chaparral species *Adenostoma fasciculatum*, *Arctostaphylos glandulosa* with the coastal sage scrub species *Salvia mellifera*, *Artemisia californica*, and *Encelia* from sites that contain *Quercus dumosa*, *Malosma laurina*, *Heteromeles arbutifolia*, and *Baccharis pilularis*. The first two principal components captured 34% of the total variation in shrub composition of these sites. The relatively low explained variation reflects the high variation among sampling points in the relative abundance of these shrub species. This variation is due to slope, aspect, and edaphic factors as well as disturbance history. Coastal sage scrub is believed to be a climax community under certain environmental conditions and a successional stage preceding chaparral under others (Mooney 1977, Westman 1979).

Seasonal and taxonomic patterns of diversity and abundance

Thirty arthropod orders were represented in the samples. The total richness of orders was higher in the pitfall samples than in the vacuum samples (29 compared to 17, spring samples; Table 1). Roughly 75% of the RTU richness in pitfall samples came from six orders: Coleoptera, Diptera, Hemiptera, Homoptera, nonant Hymenoptera, and Araneae (spiders). Approximately 90% of the RTU richness in the vacuum samples came from these orders. RTU richness and abundance within each of these orders varied among the three seasons of pitfall samples (Figs. 2 and 3). The richness and abundance of most orders and total RTU and order richness were greatest in the spring samples (Fig. 2). In the Coleoptera and Diptera winter samples were similar in abundance and diversity to the spring samples, with the fall samples less diverse and abundant. In the Hemiptera, Homoptera, Hymenoptera, and Araneae fall and winter were similar and much less diverse and abundant than spring. Notable exceptions were the Dermaptera and Collembola which were much more abundant in the winter samples than in either fall or spring pitfall samples.

Area and age relationship

Diversity and abundance in the vacuum samples generally increased with fragment area and declined with fragment age (Table 6). Total RTU richness significantly increased in larger, younger fragments (Fig. 4). Among the individual orders significant AREA-AGE multiple regressions were fit for Diptera richness and abundance, Hemiptera richness and abundance, and Lepidoptera abundance. A number of other orders had nearly significant results. Most orders showed the expected positive association with fragment area and the negative association with fragment age.

Relationships with fragment area and age were not as consistent in the pitfall samples. Total RTU or order

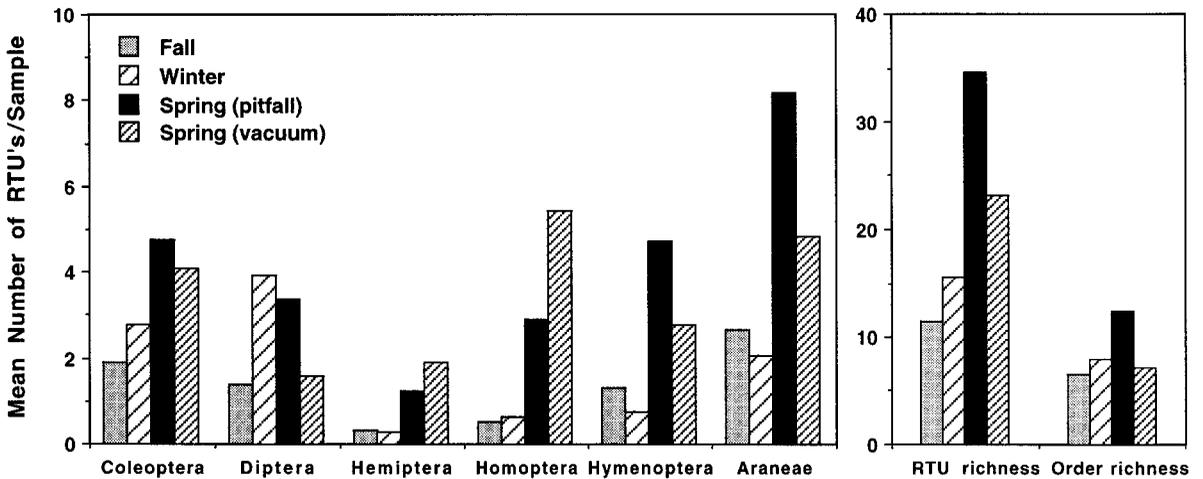


FIG. 2. The mean richness of Recognizable Taxonomic Units (RTU's) per sample in pitfall (fall, winter, spring) and vacuum (spring) samples. RTU richness is presented for the six most diverse arthropod orders, as is mean total RTU richness and mean number of orders per sample.

richness did not vary significantly with fragment area or age (Table 6, Fig. 4). There were significant positive partial regressions of Diptera richness and abundance and Microcoryphia (jumping bristletails) and Acarina abundance with area and negative partial regressions of Hemiptera richness and abundance and Hymenoptera richness with age. The strongest associations were those of spiders and these were opposite to expectations. Spider point diversity and abundance decreased with fragment area and increased with fragment age

(Table 6, Fig. 5). The other predator group examined, the carabid beetles, also increased with fragment age although not as strongly as the spiders (Table 6).

Non-native species

Pitfall samples were dominated by two non-native Isopod species (Hogue 1993) which in total comprised 30% of all individuals captured (7310 of 24 211) in the spring samples (*Armadillidium vulgare*, 24.8%, and *Porcellio laevis*, 5.4%). Two other orders dominated

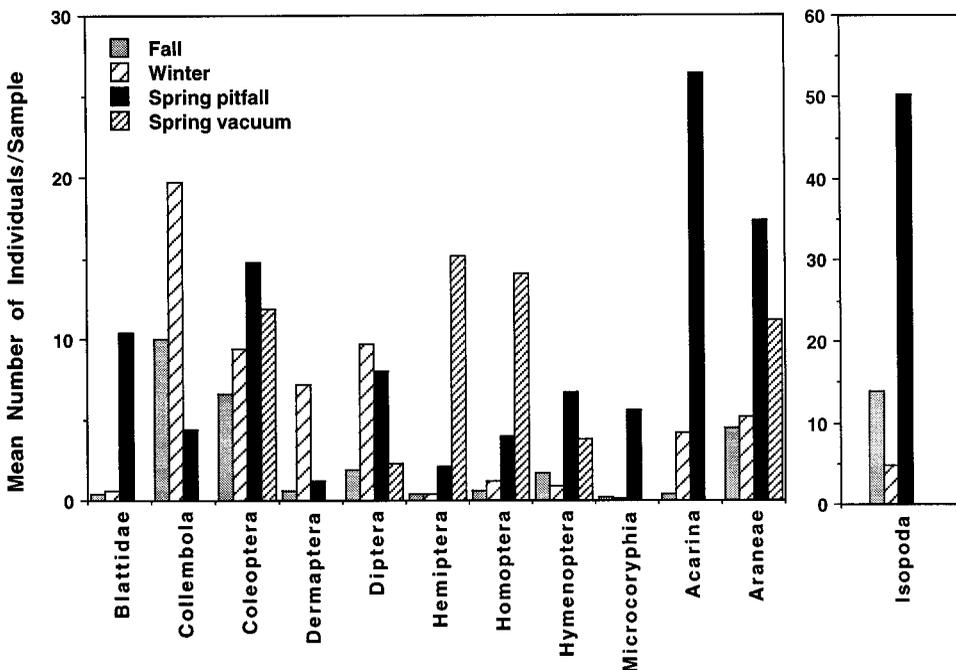


FIG. 3. The mean abundance (number of individuals) per sample in pitfall (fall, winter, spring) and vacuum (spring) samples. Mean abundance is presented for the six most diverse orders from Fig. 2 as well a number of less diverse, but abundant orders.

TABLE 6. Results of multiple regression of total RTU and order richness, total individuals, and richness and abundance within various arthropod orders on AREA and AGE of habitat fragments.

Variable	Spring (pitfall) <i>n</i> = 39				Spring (vacuum) <i>n</i> = 39			
	AREA	AGE	Model		AREA	AGE	Model	
			<i>P</i>	<i>R</i> ²			<i>P</i>	<i>R</i> ²
Total RTU richness			0.640		0.31†	-0.31†	0.003‡	0.27
RTU richness§	0.34*	-0.18	0.019	0.20				
Order richness			0.920		0.19	-0.27	0.052	0.15
Total individuals			0.260		0.24	-0.20	0.062	0.14
Individuals§	0.41*	0.07	0.052	0.15				
Coleoptera richness			0.770		0.25	-0.21	0.045	0.16
Coleoptera abundance			0.450		0.35*	-0.06	0.055	0.15
Carabid abundance	-0.06	0.38*	0.038‡	0.17				
Diptera richness	0.47**	0.10	0.022‡	0.19	0.31*	-0.35*	0.001‡	0.31
Diptera abundance	0.44*	0.13	0.044‡	0.16	0.23*	0.04	0.007‡	0.24
Hemiptera richness	-0.06	-0.57***	0.002‡	0.30	0.34*	-0.32*	0.001‡	0.31
Hemiptera abundance	0.08	-0.46**	0.007‡	0.24	0.34*	-0.25	0.001‡	0.26
Homoptera richness			0.290		0.24	-0.24	0.040	0.16
Homoptera abundance			0.320		0.39*	-0.01	0.044	0.16
Hymenoptera richness (non-ant)	0.2	-0.38*	0.006‡	0.25	0.35*	-0.05	0.067	0.14
Hymenoptera abundance (non-ant)	0.17	-0.29	0.054	0.15			0.168	
Araneae richness	-0.17	0.35*	0.015‡	0.21			0.310	
Araneae abundance	-0.23†	0.59****	<0.0001‡	0.51			0.290	
Lepidoptera richness							0.603	
Lepidoptera abundance					0.09	-0.44*	0.008‡	0.23
Acarina abundance	0.47**	0.02	0.013‡	0.21				
Microcoryphia abundance	0.50**	-0.21	0.000‡	0.38				
Non-natives								
Blattaria abundance	-0.05	0.45**	0.010‡	0.23				
Dermaptera abundance	-0.53**	0.2	0.001‡	0.43				
Isopoda abundance			0.260					

Notes: Standardized partial regression coefficients are presented for significant (or nearly significant) models (before Bonferroni correction). The *P* value for each variable and the *P* for the overall model are presented. Significance tests for overall models are adjusted by a sequential Bonferroni correction (see *Methods*).

† *P* < 0.10, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001, **** *P* < 0.0001.

‡ Significant at alpha = 0.05 after sequential Bonferroni correction. See *Methods*.

§ Without Araneae, Dermaptera, Isopoda, and Blattaria.

by introduced species were also numerous. The Blattaria comprised 6.1% of all individuals and was dominated by the introduced Oriental cockroach (*Blatta orientalis*, 92% of all Blattaria). The Dermaptera were most abundant in the winter samples (Fig. 3) when they accounted for 8.8% of all individuals, and were represented by a single, non-native species, the European Earwig (*Forficula auricularia*). Blattids increased significantly in abundance with fragment age and Dermaptera declined in abundance with fragment area. Abundance of the Isopoda was independent of fragment area and age.

After the non-native and positively responding orders (Spiders, Dermaptera, Blattaria, and Isopoda) are subtracted from total pitfall RTU richness a significant AREA-AGE model could be fit suggesting that the remaining groups do respond to fragment area and age in the expected way.

Among sample point ANOVA

Significant differences between the edge and interior of large fragments in the abundance and diversity within orders were rare. Only the Microcoryphia were significantly lower in abundance near the edge of large

fragments than they are in the interior of large fragments (Table 7). None of the vacuum sampled orders showed a significant difference between edge and interior areas at this level of aggregation.

Isopod abundance was highly variable (Table 7). Mean abundance is highest in small fragments and intermediate in edge sites. However, with the high level of variation the ANOVA is not significant. Seven samples contained over 150 Isopods (range: 265-890). Six of the seven were in small fragments, the seventh was an edge location. When these six highly abundant sites are removed, Isopod abundance is similar in the three location types (means: small 26.8, edge 26.9, interior 24.8). Although maximal Isopod abundance may be related to fragment size, mean abundance appears unrelated to fragment size or edge proximity.

*Among sample point analysis:
vegetation and disturbance*

In general, the diversity and abundance of pitfall-trapped arthropods was better predicted by the sample point variables than were the vacuum-sampled arboreal arthropods (Table 8). In the spring vacuum samples significant multiple regression models were fit for only

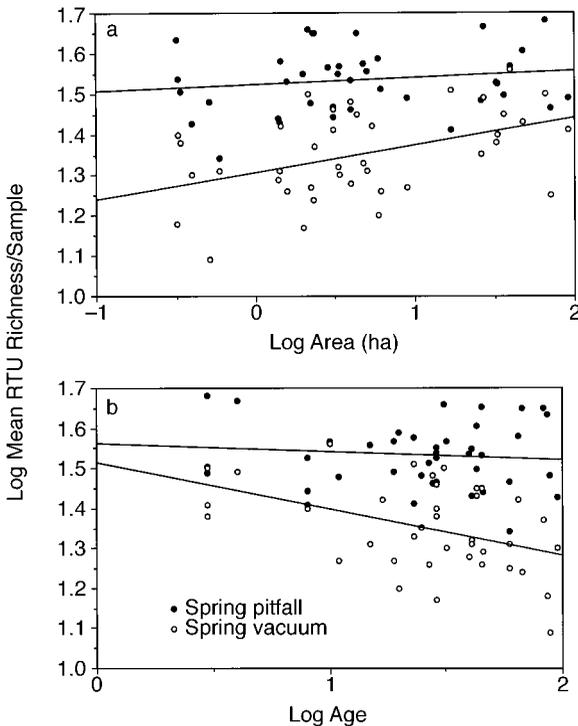


FIG. 4. (a) Logarithmic regressions of mean total RTU richness per sample per fragment on area of native shrub vegetation within the fragment. Regressions for spring pitfall ($y = 1.521 + 0.017x$, $R^2 = 0.02$, $P = 0.36$) and spring vacuum samples ($y = 1.306 + 0.068x$, $R^2 = 0.20$, $P < 0.01$) are presented. (b) Logarithmic regressions of mean total RTU richness per sample per fragment on fragment age. Regressions for spring pitfall ($y = 1.561 - 0.020x$, $R^2 = 0.01$, $P = 0.53$) and spring vacuum samples ($y = 1.514 - 0.116x$, $R^2 = 0.20$, $P < 0.01$) are presented.

total individuals and Coleoptera RTU richness and abundance. Total RTU richness could not be predicted from the sample point variables (Table 8). For the spring pitfall samples significant multiple regression equations were fit for total RTU richness, total individuals, and the RTU richness and/or abundance of a number of arthropod orders (Table 8).

The composition of the shrub vegetation was clearly an important correlate of diversity and abundance in a number of orders. Of the 14 significant models fit, nine contained significant negative partial regressions on PC1 (sites with high values of PC1 have greater cover of chaparral shrub species vs. coastal sage scrub species). Another two had marginally significant relationships with PC1. There were also four significant (and two marginally significant) negative partial regressions on PC2. Shrub species diversity (SWDIV) had four (plus six marginally significant) significant positive partial regressions. All three of these variables describing the composition of the shrub vegetation were significant terms in the model for total RTU richness in the pitfall samples. Total shrub cover was positively related to Coleoptera, Diptera, and Hymenoptera RTU

richness in the pitfall samples. The cover of exotic vegetation had significant positive partial regressions with total RTU richness, Diptera abundance, and were marginally positively associated with Coleoptera richness and Isopod abundance.

In terms of the magnitude of the standardized coefficients and the associated P values the strongest relationships were often with the abundance of the Argentine ant. Ten of the 14 significant models contained a significantly negative AA term. In the pitfall samples total RTU richness and the total number of individuals were significantly negatively associated with Argentine ant abundance. Among the orders, Coleoptera, Hemiptera, and non-ant Hymenoptera RTU richness, Diptera richness and abundance, and Microcoryphia and Acarina abundance were all negatively related to Argentine ant abundance.

Several orders showed a positive partial association with edge. Coleoptera (vacuum), Diptera, and non-ant Hymenoptera (marginally significant) had a significant negative relationship with EDGEDIST (i.e., decreased with increasing distance from an edge). Interestingly, the Diptera and Hymenoptera also have a negative relationship with AA whose abundance increases near edges (Suarez et al. 1998). So despite the tendency in these orders to increase in abundance and/or diversity near edges, Argentine ants still appear to exert a negative partial effect (Table 8). Only the Collembola had

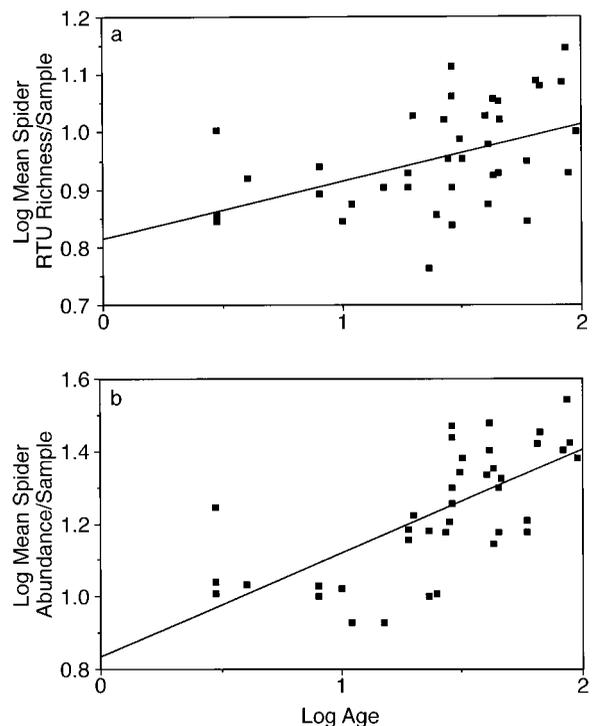


FIG. 5. Logarithmic regressions of (a) mean spider RTU richness ($y = 0.813 + 0.099x$, $R^2 = 0.183$, $P < 0.01$) and (b) mean spider abundance ($y = 0.831 + 0.286x$, $R^2 = 0.466$, $P < 0.0001$) per sample per fragment on fragment age.

a significant positive relationship with EDGEDIST (Table 8).

Predators

Significant stepwise multiple regression models were fit for carabid and spider abundance at the fragment and sample point level (Table 9). Each of the models included a positive term for the abundance of at least one of the non-native orders or Argentine ants. The abundance of the most abundant spider (ANOVA: $df = 3, 145; F = 4.89; P = 0.003$) and the most abundant carabid (ANOVA: $df = 3, 144; F = 5.78; P = 0.0009$) are significantly positively associated with the abundance of Argentine ants (Fig. 6).

Jaccard similarity analysis suggests that the differences in diversity between large and small fragments are not due to edge-induced changes in the spider and carabid community (Table 10). If they were, we would expect edge–small similarity to be greater than edge–interior similarity. This is not the case for either taxa (Table 10). If the composition of these groups changes simply as a function of fragment size then we would expect small–small similarity to be greater than both interior–small and edge–small. This is true for carabids and in spiders only the small–small vs. interior–small difference is significant. This suggests that carabid, and to a lesser extent spider, assemblages in small fragments are somewhat distinct from those in the edge or interior of larger fragments.

DISCUSSION

Our results suggest that the response of arthropods to habitat fragmentation in southern California is complex. We find evidence for strong effects of fragment age and area, edge effects, and an effect of the non-native Argentine ant. Some predator species and common non-native species appear to be enhanced by fragmentation.

Effects of fragment area and age

Point diversity and abundance in most vacuum sampled orders was correlated with fragment area (positive) and age (negative) (Table 6). We infer from the AGE result that arthropod diversity and abundance are not in equilibrium and decline over time in habitat fragments. The pitfall arthropods had more varied relationships with fragment area and age. Several individual orders (Acarina, Microcoryphia, Diptera, non-ant Hymenoptera, Hemiptera) show either positive relationships with area or negative relationships with age. However, spiders and the non-native Dermaptera and Blattaria increased with age or increased with decreasing fragment area. Area and age were not significant predictors of total pitfall arthropod diversity and abundance (exclusive of ants), however, with spiders and the non-native orders removed, total RTU richness and total individuals have a significant positive relationship with fragment area.

The ground-dwelling fauna of these fragments appears greatly altered by non-native species. In addition to Argentine ants, the Dermaptera, Isopoda, and Blattaria are a significant component of the ground-dwelling arthropod fauna of these habitat fragments. Unlike the Argentine ants, these non-native species do not appear to be restricted to edges (Tables 7 and 8). As abundant detritivores (Isopoda and Blattaria), predators (Dermaptera), and prey, these species may have a significant influence on ecosystem processes and trophic interactions, particularly in smaller and older fragments.

The vacuum arthropods seem to show a more generalized decline with fragmentation than do the pitfall samples and are not characterized by abundant non-native species or increases in spiders. Of course, at this level of taxonomic analysis we cannot rule out that many of the less abundant taxa captured in the vacuum, as well as pitfall, samples are non-native as well. We assume that because the vacuum samples are collected from a single shrub species they contain a more specialized selection of arthropods relative to the sample of ground-active arthropods captured in pitfall traps. In this specific microhabitat it is less likely that non-native species will establish or that generalist native species will be enhanced by fragmentation. Also, the absence of buckwheat in the surrounding urban matrix may increase the isolation of these populations, possibly promoting fragment-wide extinction.

We found that two predator groups, spiders and carabid beetles, were more abundant in smaller and older fragments (Table 6, Fig. 5). Abundance of spiders and carabid beetles was correlated with the abundance of the common non-native taxa, Argentine ants, Dermaptera, Isopoda, and Blattaria (Table 9). The abundance of the most common spider and carabid, both of which increase in smaller fragments, is strongly associated with Argentine ant abundance (Fig. 6). The increase in these predators could be a secondary effect of the increase in these common non-native species; adults or immatures may be prey for spiders and carabids. Alternatively, the increase in these predators and the non-native species could be due to fragmentation-induced changes in their natural enemies. They could also all be responding positively to a more productive detrital food web. Smaller fragments and edge areas have higher cover of non-native grasses. These grasses produce abundant, labile litter (Jackson et al. 1988) that should increase the abundance of members of the detritus food web (Chen and Wise 1999). These correlations suggest interesting relationships between predators and non-native species that require further study.

Similarly, Didham et al. (1998b) found that the proportion of predator species in the beetle fauna increases near tropical forest edges. Webb (1989) found a negative relationship between point diversity and area, similar to that demonstrated here for spiders and carabids, for Coleoptera in fragments of heathland. In

TABLE 7. Results of ANOVA of total RTU and order richness, total individuals, and richness and abundance within various arthropod orders.

Variable	Spring pitfall				
	Mean (SD)			Model	
	Small N = 80	Edge N = 37	Interior N = 32	F	P
Total RTU richness	35.8 (8.9)	36.4 (12.1)	36.4 (10.1)	0.0	0.9797
RTU richness†	24.1 (9.1)	26.8 (9.6)	26.6 (9.1)	1.0	0.3810
Order richness	12.3 (2.1)	12.4 (2.4)	12.9 (1.9)	1.1	0.3463
Total individuals	182.0 (170.0)	143.9 (115.4)	127.2 (69.9)	2.0	0.1367
Individuals†	82.2 (57.0)	87.4 (61.1)	84.9 (51.0)	0.4	0.7442
Coleoptera richness	5.6‡ (3.3)	4.1‡ (2.6)	4.7 (2.9)	3.5	0.033
Coleoptera abundance	20.3‡,§ (32.2)	10.3‡ (10.7)	11.7§ (22.8)	5.4	0.0053
Carabid abundance	9.3‡ (20.8)	3.9 (8.1)	0.7‡ (1.7)	7.4	0.0009
Diptera richness	3.5 (2.7)	4.6 (3.1)	3.9 (2.5)	1.9	0.1536
Diptera abundance	8.3 (10.8)	12.2 (10.2)	10.1 (15.2)	2.6	0.0797
Hemiptera richness	1.1 (1.2)	1.1 (0.9)	1.6 (1.3)	2.3	0.1021
Hemiptera abundance	2.0 (2.7)	2.0 (2.6)	2.6 (2.7)	1.5	0.2295
Homoptera richness	3.1 (2.2)	3.3 (1.7)	2.8 (1.8)	0.7	0.4925
Homoptera abundance	4.4 (3.3)	4.8 (2.8)	3.7 (2.7)	1.3	0.2813
Hymenoptera richness (non-ant)	4.3‡ (2.9)	6.2‡ (3.5)	5.5 (3.8)	4.1	0.0186
Hymenoptera abundance (non-ant)	6.4 (5.6)	8.4 (5.1)	7.9 (7.5)	2.8	0.0655
Araneae richness	8.7‡ (2.7)	7.3‡ (3.1)	7.3 (2.7)	4.6	0.0113
Araneae abundance	19.7‡,§ (10.1)	14.5‡ (9.7)	12.6§ (6.5)	8.0	0.0005
Lepidoptera richness	0.5 (0.7)	0.5 (0.7)	0.5 (0.8)	1.7¶	0.6391
Lepidoptera abundance	0.7 (1.4)	0.5 (0.7)	0.5 (0.8)	2.7¶	0.4447
Acarina abundance	25.5 (40.5)	33.0 (51.0)	27.8 (25.4)	3.5	0.032
Collembola abundance#	18.9 (40.3)	12.8 (36.5)	45.9 (62.8)	16.8¶	0.0002
Microcoryphia abundance	4.1‡ (5.1)	9.7§ (19.9)	11.8‡,§ (13.2)	11.1	<0.0001
Non-natives					
Blattaria abundance	15.1 (32.0)	3.7 (9.2)	4.5 (9.2)	9.3¶	0.0261
Dermaptera abundance#	10.3 (13.3)	1.0 (2.4)	0.2 (0.6)	31.3¶	<0.0001
Isopoda abundance	63.2 (142.6)	38.2 (77.1)	24.8 (30.4)	0.2	0.7994

Notes: Treatments are sample location types (small fragment, edge of large fragment, and interior of large fragment, see *Methods*). Analyses were performed on log-transformed data, but untransformed means (SD) are presented for clarity. Significance tests are adjusted by a sequential Bonferroni correction (see *Methods*). Within a row and sample type, means sharing the same symbol (‡ or §) are significantly different (at the $\alpha = 0.05$ level) by Tukey-Kramer HSD multiple comparisons tests.

- † Without Araneae, Dermaptera, Isopoda, Blattaria.
- ‡ Significantly different (at the $\alpha = 0.05$ level) from other means in the same row and sample type sharing this symbol.
- § Significantly different (at the $\alpha = 0.05$ level) from other means in the same row and sample type sharing this symbol.
- || Significant at $\alpha = 0.05$ after sequential Bonferroni correction. See *Methods*.
- ¶ Chi-square approximation from Kruskal-Wallis test. Analyzed with nonparametric test because data could not be normalized. Post-hoc comparisons not possible.
- # Winter data analyzed (see *Methods*). Sample sizes = 64, 20, and 17.

that landscape there is a high diversity of edge species and small fragments are dominated by the edge fauna. Our results suggest this is not the case here as the spider and carabid species composition in the interior of large fragments is similar to that near the edge (Table 10).

Taken together these results suggest that arthropod fauna of smaller and older fragments is much different than that in larger and younger fragments. The density and point diversity of arboreal arthropods on California buckwheat are generally lower in older and smaller fragments as are many pitfall sampled orders. The influence of spider and carabid predators and abundant non-native species is greater in smaller and older fragments.

Seasonal and vegetation effects

The seasonal distribution of arthropod diversity and abundance appears to reflect the seasonal variation in

rainfall characteristic of a Mediterranean climate: winter rains and summer drought (April–November). In general, abundance and diversity were lowest in the fall sample, near the end of the drought period. Total diversity and abundance, and diversity and abundance in many individual orders were higher in winter than fall (Figs. 2 and 3), possibly due to the onset of winter rains. Diversity and abundance were at their maximum in the spring samples when conditions of temperature and moisture were apparently best for arthropod activity and productivity.

In general pitfall arthropod diversity and abundance was negatively related to the abundance of chaparral shrub species and positively associated with the coastal sage scrub species (Tables 5 and 8). Diversity and abundance in some orders was also positively correlated with the diversity of shrub species, the percent cover of native shrub species, and the cover of non-woody

TABLE 7. Extended.

Spring vacuum				
Mean			Model	
Small N = 75	Edge N = 39	Interior N = 32	F	P
21.8‡ (8.2)	28.1‡ (8.3)	27.0 (11.7)	6.5	0.0019
...
6.9‡ (1.4)	7.7‡ (1.1)	7.2 (1.3)	5.0	0.0079
46.8‡ (31.0)	67.9‡ (35.3)	67.9 (50.2)	6.8	0.0015
...
3.6‡ (2.5)	5.3‡ (2.8)	4.8 (3.0)	6.6	0.0018
8.6‡§ (8.9)	16.9‡ (12.1)	20.0§ (30.6)	10.5	0.0001
...
1.2‡§ (1.2)	2.3‡ (1.7)	2.5§ (2.8)	7.4	0.0009
1.7‡ (2.2)	3.8‡ (5.2)	3.6 (4.5)	6.6	0.0019
1.8‡§ (1.9)	2.4‡ (1.3)	2.6§ (1.5)	6.4	0.0022
4.2‡ (5.1)	7.4‡ (10.5)	6.4 (6.4)	4.9	0.0086
5.3 (3.0)	6.2 (3.4)	6.2 (2.9)	2.1	0.1224
13.3 (16.9)	16.8 (15.3)	18.9 (17.5)	3.0	0.0505
2.5‡ (2.0)	4.2‡ (3.2)	4.0 (4.1)	3.3	0.0382
3.4 (3.6)	5.9 (5.6)	5.4 (6.4)	3.1	0.0487
5.2 (2.9)	4.2 (2.5)	4.2 (2.8)	2.7	0.0676
11.5 (12.4)	10.7 (17.4)	7.7 (8.5)	2.3	0.1026
1.1‡ (1.1)	1.9‡ (1.2)	1.6 (1.0)	6.5	0.002
1.9‡ (2.1)	3.8‡ (5.7)	3.5 (3.6)	4.6	0.0118
...
...
...
...
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...

exotic vegetation (Table 8). Perhaps because the vacuum samples were collected from a single shrub species, the vacuum-sampled arthropods showed little relationship with surrounding vegetation structure and composition.

Effect of Argentine ants

Previous analyses of the ants in these samples demonstrated a strong negative association of native ants with Argentine ants (Suarez et al. 1998). The data presented here suggest that Argentine ants also cause reductions in diversity or abundance of non-ant arthropods (Table 8). Several previous studies have reported effects of Argentine ants on native arthropods (Cole et al. 1992, Human and Gordon 1997), while others have found no effect (Holway 1998b). A problem with a number of these studies (including ours) is that the presence of Argentine ants is often confounded with other disturbance factors. In California, Argentine ants invade natural habitat along edges with human land uses (Suarez et al. 1998, Human and Gordon 1997). Presumably, proximity to an edge is correlated with many other ecological changes independent of the Argentine ant. Human and Gordon find differences in the arthropod community at the Jasper Ridge reserve at Stanford, California, USA; however, they admittedly compared edge areas with Argentine ants to interior

areas lacking Argentine ants without controlling for other edge effects. Holway looked at the effect of Argentine ants on arthropods in riparian habitat near Davis, California, USA, where the distribution of Argentine ants is patchy, but apparently unrelated to edge or anthropogenic disturbance. In comparing areas with and without Argentine ants he found large effects on native ants, but no effect on non-ant arthropods. Cole et al. (1992) present compelling evidence of an effect of Argentine ants on native arthropods in Hawaii. However, Hawaii lacks a native ant fauna which may exacerbate the effects of the introduction of Argentine ants making the extrapolation of their results to a continental setting uncertain.

We also face the problem of potentially confounding variation. We have attempted to disentangle the effects of Argentine ants from other disturbances through extensive sampling along an edge-interior gradient and multiple regression analyses that incorporate variables that capture some of the variation in disturbance. Our inference is strengthened by the fact that there are positive edge effects in several taxa, yet the partial effect of Argentine ants is negative (Table 8). The apparent relationship of abundant spider and carabid predators with Argentine ants raises the possibility that the negative correlation of Argentine ants with other arthropods could be due to indirect effects mediated through predators. Experimental and mechanistic approaches will be required to more thoroughly understand the interaction between Argentine ants and non-ant arthropods.

The mechanisms by which the Argentine ants might affect the orders we examined are currently unknown. Argentine ants interfere in the foraging activity of other ant species (Human and Gordon 1996) and may do this to other arthropods. Species that are slow moving, flightless, or lacking a hard exoskeleton may be vulnerable to ant predation (Human and Gordon 1996). Argentine ants also prey upon arthropod eggs (Driestadt et al. 1986, Way et al. 1992).

There are interesting differences and similarities between our results and those of Cole et al. (1992) and Human and Gordon (1997). Both Cole et al. and Human and Gordon report negative effects of Argentine ants on spiders and suggest that Argentine ants and spiders may compete for prey. Conversely, we found spiders most abundant and diverse in the smaller, older fragments which have the highest abundance of Argentine ants. Both previous studies observed a positive association between Argentine ants and non-native Isopods, but we find no association (Table 8). Similar to our findings, Human and Gordon found a strong association of one species of carabid beetle with Argentine ants. However, Cole et al. found a weak negative association with two carabid species. Human and Gordon found negative associations of Diptera, Collembola, and Acarina with Argentine ants. We also found negative associations with Diptera and Acarina, however, our find-

TABLE 8. Results of multiple regression analysis of spring samples from the 11 largest fragments.

Variable	Sampling method	PC1	PC2	SWDIV	SHRUB	EXOTIC
Total RTU richness	Pitfall	-0.45**	-0.39*	0.23*	0.21†	0.25*
	Vacuum					
RTU richness¶	Pitfall	-0.44*	-0.39*	0.21†	0.31*	0.21†
Order richness	Pitfall					
	Vacuum					
Total individuals	Pitfall	-0.58***	-0.64***	0.27*		
	Vacuum					
Individuals¶	Pitfall	-0.49**	-0.62***	0.23*	0.33**	
Coleoptera richness	Pitfall				0.33*	0.24†
	Vacuum			0.28*		
Coleoptera abundance	Pitfall	-0.27†				
	Vacuum			0.24†		
Diptera richness	Pitfall	-0.31*	-0.29†	0.23†	0.25*	
	Vacuum					
Diptera abundance	Pitfall	-0.26†		0.22†		0.24*
	Vacuum				0.44**	
Hemiptera richness	Pitfall					
	Vacuum					
Hemiptera abundance	Pitfall					
	Vacuum					
Homoptera richness	Pitfall					
	Vacuum					
Homoptera abundance	Pitfall					
	Vacuum					
Hymenoptera richness (non-ant)	Pitfall	-0.44**		0.18†		
	Vacuum					
Hymenoptera abundance	Pitfall	-0.51**		0.19†		
	Vacuum					
Araneae richness	Pitfall					
	Vacuum					
Araneae abundance	Pitfall					
	Vacuum					
Lepidoptera richness	Vacuum					
Lepidoptera abundance	Vacuum					
Acarina abundance	Pitfall	-0.39*	-0.66***	0.31*		
Microcoryphia abundance	Pitfall	-0.40*	-0.36†			
Collembola abundance§,	Pitfall-winter					-0.40**
Non-natives						
Blattaria abundance§	Pitfall	0.23*	-0.28**			
Dermoptera abundance§,	Pitfall-winter			0.44**		0.27†
Isopod abundance	Pitfall	-0.57**	-0.58**			0.24†

Notes: Total RTU and order richness and total number of individuals and richness and abundance within various arthropod orders were regressed on variables describing sample points. Standardized partial regression coefficients are presented for significant variables in significant (or nearly significant) models (before Bonferroni correction). The *P* value for each variable and the *P* for the overall model are presented. Significance tests for overall models are adjusted by a sequential Bonferroni correction (see Methods); *n* = 64 sample points for spring pitfall traps and 69 locations for spring vacuum samples.

† *P* = 0.05–0.10, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001, **** *P* < 0.0001.

‡ Significant at alpha = 0.05 after sequential Bonferroni correction. See *Methods*.

§ Analyzed with bivariate Spearman rank correlations because of nonnormality.

|| Sample size for winter is 33 sample points.

¶ Without Araneae, Dermoptera, Isopoda, Blattaria.

ings suggest that Collembola are negatively associated with edges, but not Argentine ants (Table 8). Studies of the impact of an edge-invasive species such as the Argentine ant need to explicitly consider other edge effects which could potentially obscure a real effect or create an apparent effect.

Relative influence of area and edge

Surprisingly, we found little evidence of strong associations with edge (positive or negative) aside from those that appear to be related to the Argentine ant. Only the Collembola showed a pattern of lower density

near edges that was apparently independent of the Argentine ant (Table 8). Many of the orders that are less abundant in smaller fragments do not show negative associations with edge (Table 7). Similarly, the increase in spiders, Dermoptera, and Blattaria in smaller fragments does not appear to be due to a positive association with edge. Two orders, the Diptera (pitfall) and Coleoptera (vacuum), have a tendency to increase near edges, but this increase can apparently be counteracted by Argentine ants (Table 8).

Edge effects, other than the Argentine ant, may be important but their effects on abundance could be ob-

TABLE 8. Extended.

EDGEDIST	AA	Model	
		<i>P</i>	<i>R</i> ²
	-0.49***	0.001‡ 0.247	0.34
	-0.52***	0.000‡ 0.130 0.294	0.39
	-0.38**	0.001‡ 0.133	0.35
	-0.59****	0.000‡	0.42
	-0.35*	0.043	0.22
	-0.29*	0.001‡ 0.255	0.31
	-0.33*	0.000‡	0.34
	-0.41**	0.002‡ 0.284	0.32
	-0.37**	0.000‡ 0.229	0.39
	-0.46**	0.010‡ 0.594 0.132 0.791 0.241 0.167 0.245 0.179	0.27
	-0.21†	0.000‡ 0.175 0.000‡ 0.294 0.361 0.387 0.177 0.416 0.346 0.366	0.39 0.39
		0.005‡ 0.017‡	0.29 0.31
	0.44***	0.229	
	0.18†		
		0.005‡	0.31

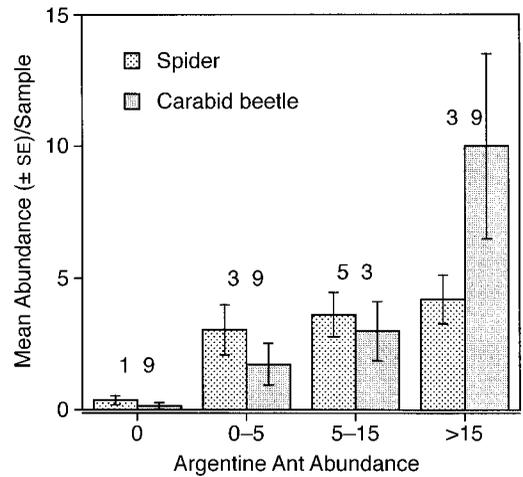


FIG. 6. The abundance of the most abundant Carabid beetle species and the most abundant spider species as a function of Argentine ant abundance (mean number of Argentine ants captured at that sample point). Numbers above columns are the number of pitfall locations.

scured by dispersal of arthropods between edge and interior areas. Similarly, if multiple edge effects have opposing influences on arthropod abundance and diversity (as they appear to have in the Diptera and Coleoptera) then they may be undetectable by looking at abundance. Alternatively these fragments, even the largest ones, may be all edge for these arthropods. Or, edge effects could be scale-dependent (Donovan et al. 1997) and only manifest in small fragments (<30 ha) which are predominantly edge (assuming a 100 m edge effect) in which case their effect is indistinguishable from an area effect.

Alternatively, whole-fragment attributes, such as the influence of area on extinction rate, may be a more important influence on point abundance and diversity than edge effects. The observed patterns might also

TABLE 9. Results of stepwise regression analysis on spider and carabid beetle abundance and diversity in 39 habitat fragments (spring samples) and among 62 sample points.

Model type	Variables in model	Standardized coefficient	<i>F</i>	df	<i>P</i>	<i>R</i> ²
Carabid abundance	ISOPODA	0.55****	20.7	2, 36	<0.0001	0.57
	DERMAPTERA	0.38**				
among sample points	ISOPODA	0.43***	13.2	2, 58	<0.0001	0.31
	AA	0.34**				
Spider abundance	AGE	0.52****	21.6	3, 35	<0.0001	0.68
	DERMAPTERA	0.32**				
	ISOPODA	0.29**				
among sample points	ISOPODA	0.44***	7.9	3, 58	0.002	0.21
	PC1	0.30*				

Notes: Variables available to be entered into the model were AGE, AREA, and the abundance of the exotic-dominated orders: Blattaria, Dermaptera, and Isopoda and Argentine ants. Only the variables entered into the model (*P*-to-enter = 0.05) are listed, in the order they entered the model.

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001, **** *P* < 0.0001.

TABLE 10. Mean Jacard similarity coefficients for 11 carabid beetle species and 12 spider species from the spring pitfall samples.

Taxon	Small/ small	Small/ edge	Edge/ edge	Edge/ interior	Interior/ interior	Interior/ small	Chi- square	df	P
Carabids	0.33 ^{1,2,3}	0.21 ^{1,4}	0.21 ^{2,5}	0.25 ^{1,6}	0.29 ^{4,5,7}	0.21 ^{3,6,7}	277.2	5	<0.0001
N	(1378)	(1537)	(406)	(648)	(253)	(1219)			
Spiders	0.30 ^{1,2}	0.30 ^{3,4}	0.31	0.28	0.25 ^{1,3}	0.25 ^{2,4}	50.8	5	<0.0001
N	(2485)	(1917)	(351)	(675)	(300)	(1775)			

Notes: Coefficients represent the pairwise similarity in samples collected at three types of locations: small fragments, within 100 m of the edge of larger fragments, and >100 m into the interior of larger fragments. Heterogeneity among comparison types was tested by a Kruskal-Wallis ANOVA. Coefficients that share the same superscript are significantly different, at $\alpha = 0.05$ (sequential Bonferroni-corrected) by Mann-Whitney *U* test. *N* is the number of pairwise comparisons made among sample points.

result from changes in natural enemies, such as the vertebrate insectivore community, that occur as a function of fragment size.

In fragmented forest systems, abiotic and biotic edge-interior gradients have been demonstrated (see review in Murcia 1995). In coastal sage scrub fragments exotic herb and grass cover (Table 4) and the abundance of Argentine ants increase near edges (Suarez et al. 1998), however, physical gradients have not been measured and may be much different than in forest fragments. We suspect the existence of a gradient in moisture and nutrients associated with runoff from backyards and impermeable surfaces. A moisture subsidy could be very important in this semiarid region. It seems likely that moisture availability is what limits Argentine ants to the edge of the fragments (Tremper 1976, Majer 1994, Holway 1998a, Suarez et al. 1998).

Conclusions

We find evidence that area, edge, and secondary effects of fragmentation affect the arthropod community in scrub habitat in coastal southern California. The abundance and diversity of many arthropod orders collected on California buckwheat and in pitfalls were lower in smaller and older habitat fragments. This, and the large changes in the abundance of Argentine ants, spider and carabid predators, and non-native detritivores, portend changes in trophic relationships, pollination, herbivory, and nutrient cycling as a consequence of fragmentation. It is reasonable to expect that these changes will cause secondary effects both within the arthropods and on plants and vertebrates, and that alteration of ecosystem functions may occur.

The order-level patterns that we have described certainly must obscure variation in species-specific responses to fragmentation and edge. Indeed, these results show that responses are complex even at the level of order. Our results should only be considered representative of fragments of coastal sage scrub that are of similar size and age range. Further comparisons with larger fragments and unfragmented blocks of habitat are needed to extend our results. Arthropods are notoriously variable in space and time (Ito 1980, Schultz and Chang 1998). This is undoubtedly at least partly

responsible for the relatively low R^2 values in our regression analyses. However, the lack of stronger relationships with these variables does leave open the possibility that important effects have been obscured by intrinsic variability.

Conservation planning in this region has focused on coastal sage scrub rather than chaparral because of its high plant and vertebrate diversity and endemism. Our results suggest that point diversity and abundance of arthropods is also greater in coastal sage scrub than in chaparral. However, we have not analyzed differences in species composition and cannot evaluate the relative conservation significance of the species in each vegetation type.

The changes observed in the arthropod community suggest that fragmentation may affect food availability and thus habitat suitability for insectivorous vertebrates. These changes could be partly responsible for the decline in diversity of insectivorous birds in these fragments (Soulé et al. 1988, Bolger et al. 1991, Crooks et al., *in press*). However, interpretations of our results for insectivores in these fragments should be tempered by recognition of the coarseness of our taxonomic analysis and the general lack of knowledge of the diets of vertebrate insectivores. The abundance of particular species, genera, or families of arthropods may be more important to these species than overall diversity and abundance. Also, increases in non-native arthropods could potentially provide alternative prey choices and offset some losses of other prey species. More detailed taxonomic and diet analyses will be necessary to further evaluate the effect of habitat fragmentation on vertebrate food availability.

The results presented here support the view that Argentine ants are a significant conservation threat to the arthropod fauna of the region. However, further research is needed to mechanistically link Argentine ants to declines in non-ant arthropods.

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